defenses, and *P. spinicola*'s added defenses may contribute little to plant health. *P. spinicola* may lose part of its competitive edge under high light conditions because *P. flavicornis* and other acacia ant species that expend less energy on defense have higher net energy gains than *P. spinicola*.

Acacia trees survive and grow poorly under low light conditions (Janzen 1983). The added defense of *P. spinicola* may contribute little to acacia health where light is too low to support acacia growth and survival. *P. spinicola* may again lose some competitive advantage by having lower net energy gains than species that expend less energy on plant defense. Under moderate light conditions the added defenses of *P. spinicola* may increase plant health. In this intermediate range where *P. spinicola*'s added effort presumably leads to higher energy rewards from the tree, *P. spinicola* is most competitively dominant over all other acacia ant species.

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WHY BUTTRESSES?
THE LITTER TRAP THEORY

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Abstract. We propose an additional theory for the advantage of buttresses on tropical forest trees: cross-slope buttresses facilitate organic matter accumulation at the base of the tree which (1) increases the amount of nutrients directly available to the tree and (2) acts to decrease erosion. We tested one aspect of this litter trap theory by examining the relative investment in cross-slope "litter trap" buttresses and down-slope "support" buttresses. We predicted that the length of cross-slope "litter trap" buttresses would be greater than the length of down-slope "support" buttresses. We found no significant difference in the lengths of cross-slope and down-slope buttresses, which does not allow us to distinguish between the litter trap and structural functions . It is possible that both are equally important.

INTRODUCTION (NEP)

Very few questions in tropical ecology have engendered as much speculation as: "why do some trees have buttresses?" Though few buttressed trees exist in temperate regions, well-buttressed trees commonly occur in the tropical forests of Costa Rica.

Past research has focused on the structural advantages conferred by buttressing. Buttresses are more common in wind and gravitationally-stressed habitats than in less stressed habitats (Bansak et al. 1993). Henwood (1973) and Ennos (1993) suggest that buttresses should develop along the axis of stress and should act to reduce tension on roots such that they are less susceptible to breakage and withdrawal. Additional hypotheses include (1) buttresses increase the surface area at the base of the tree and thus should increase the potential for gas exchange (Blundell, pers. comm.), (2) buttresses act as conduction shortcuts between the roots and the trunk of the tree (Richards 1952), (3) buttressed trees occupy a greater forest floor area and thus should have a competitive advantage for space over non-buttressed trees (Black and Harper 1979), and (4) buttresses inhibit the growth of lianas (Black and Harper 1979).

As an additional hypothesis, we propose that buttresses which are perpendicular to local slope act as litter traps and facilitate the accumulation of organic matter immediately surrounding the tree. We predict that these cross-slope buttresses increase immediate nutrient availability and act to decrease erosion at the base of the tree. We tested one aspect of the litter trap theory by examining the relative investment in cross-slope "litter trap" buttresses and down-slope "support" buttresses. Presumably, greater investment in down-slope buttresses suggests the greater relative importance of the structural function, whereas greater investment in cross-slope buttresses suggests the greater importance of the litter trap function. We predicted that on the steep slopes of the Monteverde cloud forests, cross-slope buttresses would be longer than down-slope buttresses.

METHODS (IJS)

Our survey was conducted on 20 January 1995 in primary growth cloud forest, approximately 0.5 km from the Estación Biologica Monteverde, Costa Rica. We sampled a 420 m trail-transect along the steep Pacific side of the continental divide. To minimize effects of trail disturbance, we sampled only on the slope above the trail. All buttressed trees within sight and at least 3 m from the trail were surveyed.

A buttressed tree was defined as any tree where (at least one) buttress length at 50 cm

above the ground was greater than or equal to 150% of the diameter at breast height (Fig. 1, a). We excluded trees with multiple boles, strangler fig parasites, or rotting buttresses.

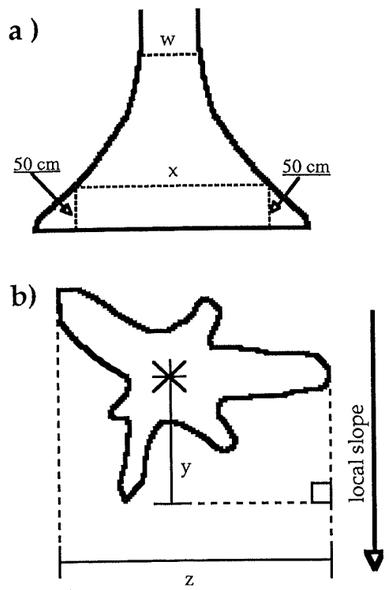

FIG. 1. Criteria for buttresses measurements.
a) Down-slope view, definition of a buttressed tree. w= dbh, x= buttress length at 50cm height. Buttressed trees were defined as trees where x≥1.5(w).
b) Aerial view, lengths of cross-slope (z) and down-slope (y*2) buttress faces.

For our principal measurements, to distinguish between an exposed or undercut root and a buttress, we defined both ends of a buttress face to be where buttress height was 30 cm. For each tree we measured the lengths of the buttress faces across (cross-slope) and parallel to the slope (down-slope). A buttress face was the longest dimension of buttressing in the measured plane (Fig. 1, b). Because organic matter tended to accumulate on the up-slope side of the tree, we measured only the length of the down-slope buttress from the center of the bole to the end of the buttress. This measurement was doubled as an estimate of the maximum length of the down-slope buttress face (down-slope face=2*down-slope measurement). Diameter at breast height was also recorded for each tree.

RESULTS (IJS)

The lengths of cross-slope and down-slope buttress faces were not significantly different (t=1.43, df=24, P=0.165, Table 1).

TABLE 1. Length (cm) of buttress faces oriented across (cross-slope) and parallel to (down-slope) local topographical slope. N=25.

Difference		Cross-slope	Down-slope
Mean	169.24	142.88	26.36
s.d.	125.45	105.64	92.44

We noted an insignificant trend of cross-slope faces increasing in size more rapidly than down-slope faces with increasing DBH (Fig. 2).

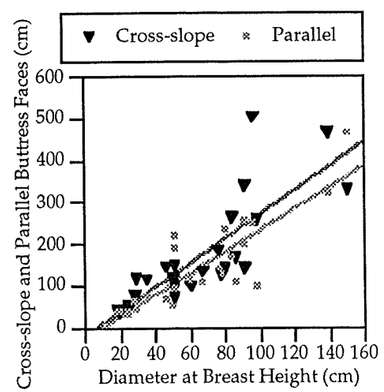

FIG. 2. Relationship between buttress lengths of cross-slope and down-slope faces to diameter at breast height (R^2 for cross-slope face=0.67, slope=2.91; R^2 for parallel slope face=0.74, slope=2.57, N=25).

DISCUSSION

Our finding that buttresses were not significantly longer along the cross-slope axis does not support our prediction. However, the argument that buttresses function primarily as structural supports is also weakened by our results. The fact that the trend is toward longer buttresses on the cross-slope axis contradicts the expectations of Henwood (1973) and Ennos (1993), who predicted that evidence for the structural function of buttresses would be an increased investment in down-slope buttresses.

Our findings, and those of Bansak et. al (1993), suggest support for equal importance of both the structural support and the litter trap functions. We found no significant difference in cross-slope and down-slope buttress lengths; similarly, Bansak et al. (1993) found no significant difference in buttress volume along any given axis.

Furthermore, Bansak et al. found a significant increase in total buttress volume with an increase in wind and gravitational stress. Because the effectiveness or importance of other proposed functions (liana inhibition, competition for space, gas exchange, and conduction short-cuts) would not be expected to increase with steeper slope or greater wind stress, they cited this finding as evidence for the importance of the structural support function. However, the effectiveness and importance of buttresses as litter traps would also be expected to increase with increasing slope, and to a lesser degree, with increasing wind stress. Thus the increase in buttressing along all axes with the increase in gravitational and wind stress seems to emphasize the potential importance of both the structural and litter trap functions, and to de-emphasize the importance of other proposed functions.

Further study is warranted to adequately assess the importance of the litter trap function. Specifically, four assumptions of litter trapping should be tested: 1) buttressed trees trap more organic matter than non-buttressed trees; 2) there is an overall greater amount of decomposition at the base of buttressed trees due to the greater pool of organic matter, and potentially due to an increased rate of decomposition due to channeling of water from the canopy to the litter pool; 3) the buttressed tree will be able to effectively utilize the increase in nutrients available from this larger pool; and 4) the build up of organic matter around the base of the tree will result in decreased localized erosion rates, and will effectively stop potential undercutting of the tree's root supports.

Buttressed and non-buttressed trees should be compared in terms of the volume of organic matter around the base of trees. It is important that such a study measure the total volume of the O horizon around the trees in relation to the surrounding slope. A greater build up around the buttressed trees would provide evidence for the reduced erosion assumption, and potentially for increased nutrient availability. Other, more difficult and more long-term studies could more clearly establish the nutrient benefits by comparing the rates of litter decomposition and nutrient release at the base of buttressed and non-buttressed trees.

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